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Speciation in modern marine bivalves (Mollusca: Bivalvia): Insights from the published record*

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Abstract: What can living marine bivalves tell us about speciation in the marine environment? Three sets of literature data on Recent marine bivalves are analyzed for insight into the mechanisms behind bivalve speciation processes. (1) A dataset of all marine bivalves described as new to science during the years 2000-2009 (381 species in 135 published papers) reveals that malacologists are still describing undiscovered biodiversity, based largely upon newly collected expedition material. New species include those of both large and small body size (0.86-500 mm, mean 28 mm), from 51 bivalve families, all oceanic basins, and a wide range of water depths (intertidal to 7,333 m, mean 444 m). External shell characters dominate the diagnoses but are increasingly supplemented by anatomical, molecular, and phylogenetic evidence. Endemism is low (2.6%) when stated as such although another 57% of species were described as (thus far) restricted to a particular geographic region, habitat, or both. High percentages of deep-water and otherwise (geographically or ecologically) restricted species, plus several case studies, suggest that physiological specialization, in the form of bathymetric limits, unique dietary adaptations, or host/symbiont associations, plays an important role in setting up barriers to gene flow in marine bivalves. (2) Bivalve species complexes [*i.e.*, closely related, cryptic (possibly sibling) species with obscure morphological boundaries, or highly variable single species] also imply factors involved in ongoing speciation. Seven recently studied marine taxa are presented in which species complexes are either revealed or resolved by molecular data. Apparent barriers to gene flow are in most cases physiological (sympatric), or (in two cases) physical (allopatric), and in one case can be readily broken down by anthropogenic transport. (3) Two recent published phylogenetic analyses are discussed that show (a) disparately sized sister taxa with their synapomorphies (glochidia in Unionoidea; chemosymbiotic bacteria and mucus-tube feeding in Lucinoidea; cruciform muscle and long siphons in Tellinoidea; aortic bulb in Veneroidea) as recognized innovations that facilitated radiation of the more species-rich sister, and (b) polytomies in Lucinoidea that suggest rapid ongoing evolutionary change in several clades. Together these three sets of published data defeat the concept of a Marine Speciation Paradox in bivalves—speciation clues are merely subtler in marine bivalves and most often act at the physiological, rather than physical, level.

Key words: taxonomy, species complex, phylogeny, allopatry, sympatry

The marine environment challenges the study of speciation because, despite high diversity in habitat, body form, lifestyle, and taxonomic category, (1) the marine realm has less effective barriers to dispersal (at least in the more traditional, terrestrial sense; one of the few exceptions might be geminate species associated with rise of the Isthmus of Panama, see Smith *et al.* 2006, Marko and Moran 2009 for recent studies) and therefore fewer opportunities for allopatric isolation (Vermeij and Grosberg 2010), and (2) the planktonic larvae produced by most marine organisms have the potential for wide dispersal and thus to maintain high levels of gene flow between populations. This is called the Marine Speciation Paradox (Bierne *et al.* 2003). Mollusca, the most species-rich phylum in the sea, provides excellent examples of this pattern. Marine bivalves, the second most species-rich class of molluscs, are particularly vexing. Whereas species of other groups of molluscs—especially landsnails and freshwater bivalves—are often restricted to one hillside or island or lake, marine bivalves are often widely distributed in what is at least superficially a more-or-less continuous, homogenous environment, and the mechanisms underlying their radiation are more difficult to comprehend. Even marine gastropods are more straightforward—unlike bivalves, many gastropods have reproductive or feeding specializations that lend themselves readily as isolating mechanisms (see Allmon and Smith 2011, Krug 2011).

To look for insight into marine bivalve speciation, especially toward resolving the presumed paradox, I have examined new species descriptions (plus the supporting data behind them), recently studied species complexes, and phylogenies published during the past decade to examine what these data can reveal (if anything) about ongoing speciation in marine bivalves. The following questions are foremost: What kinds of marine bivalves are we currently

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describing as new? Are there any groups conspicuously missing from this dataset? What criteria (morphological [shell, soft anatomical], molecular, phylogenetic) have been used to define these species as new? Do these new species descriptions reflect recently isolated species, or something else? Can we identify any groups of marine bivalves that are currently undergoing rapid speciation? Can we identify mechanisms for marine bivalve speciation in the current era?

MATERIALS AND METHODS

New species descriptions of Recent marine bivalves for the years 2000-2009, as a sample time interval in the current era, were compiled from *Zoological Record* via the online Thomson Reuters database "Web of Knowledge" (see http://wokinfo.com/), accessed through Cornell University Library. Each species was tabulated in a simple spreadsheet according to date of publication, family, geographical, and depth distribution (the latter not differentiating between live- and dead-collected specimens), maximum recorded size, endemicity (or "restriction" in geographic distribution or habitat), distinguishing characters from nearest relatives, the source of the new material (*e.g.*, new collections/expedition, taxonomic revision, etc.), and whether the original description included anatomical data, molecular data, and/or a supporting (phylogenetic or another type of numerical) analysis. Shell characters distinguishing new species from nearest relatives were further broken down into 12 categories: size, shape, color, sculpture, thickness, inflation, muscle scars/pallial line, lunule/escutcheon, hinge, ligament, prodissoconch/umbones, and periostracum. The data presented herein were generated by simple resorting of the spreadsheet according to particular columns.

RESULTS AND DISCUSSION

New species descriptions 2000-2009

New species of molluscs are being described every month, if not every week. The rate of new species descriptions per year in malacology has indeed been high since 1758 and relatively constant for at least the past century (Rosenberg 2009). For this part of the analysis, new Recent marine bivalve descriptions from the malacological literature were tabulated for the years 2000-2009, totaling 381 species by 118 authors (64 first authors) in 135 published papers (see Appendix). The mean number of species described per year during this time interval was 38.10 ± 21.59 *SD* (standard deviation) [maximum (2002): 82 in 18 papers; minimum (2000): 12 in 7 papers]. The mean number of species described per paper during this time interval was 2.83 ± 3.58 *SD* [maximum (2002): 4.56 ± 5.41; minimum (2000): 1.71 ± 1.25].

Source of the material

Malacologists are describing new species based largely (243 of 381 species, or 64%) on four broad categories: (1) new collections (see below; 132 of 381 species, or 35%), (2) taxonomic revisions (either regional or worldwide, at generic or higher taxonomic levels; 98 of 381 species, or 26%), (3) revisions of regional checklists (10 of 381 species, or 3%), or (4) commercial considerations (*e.g.*, aquaculture, harvested species; 3 species: *Tridacna costata* Roa-Quiaoit, Kochzius, Jantzen, Zibdah, and Richter in Richter *et al.*, 2008, *Anguipecten simoneae* Morrison and Whisson, 2009, and *Crassostrea hongkongensis* Lam and Morton, 2003). Many of the important new collections originated from new expeditions (especially the MUSORSTOM Project at New Caledonia and elsewhere, led by Philippe Bouchet at the Museum National d'Histoire Naturelle in Paris, *e.g.*, Dijkstra 2001, 2002, Krylova 2001, Lamprell and Healy 2001, 2002, Glover and Taylor 2007, Lutaenko and Maestrati 2007, ter Poorten 2009) or explorations of extraordinary deep-sea environments such as seamounts, seeps, and hydrothermal vents (*e.g.*, Dijkstra and Gofas 2004, Holmes *et al.* 2005, Oliver and Holmes 2006b).

Nature of the evidence

Malacologists are describing new species from material including live-collected or living animals (179 of 381, or 46%) or (slightly more so) from empty shells alone (202 of 381, or 53%). Although anatomical features when available form part of the original description in most cases (120 of 179, or 67%), these enter into diagnoses against morphologically similar species in only slightly over half of such cases (66 of 120, or 55%). This is not surprising given that bivalve shells are generally recognized as good sources of systematic data sufficient to distinguish them from congeners and other closely related forms (evidenced by the new species descriptions referenced herein). In some cases (*e.g.*, Limidae; Mikkelsen and Bieler 2003), gross soft-anatomical characters at the generic level are remarkably uniform, with diagnoses heavily reliant on external shell features and color of the living animals (both potentially affecting the impact of visual predators). This value of shell characters is also fortuitous for descriptions of fossil bivalves; in both fossils and Recent species known from empty shells alone, muscle scars and pallial lines on inner shell surfaces provide some anatomical information even in the absence of a soft body.

Within the shell characters used in diagnoses ($N = 367$), the description of *Neolepton holmergi* Zelaya and Ituarte, 2003 cited the most categories (6: size, shape, sculpture, inflation, hinge, prodissoconch/umbones, and periostracum). Another 14 species used 5 categories, 47 used 4, 77 used 3, 136 used 2, and 92 used only one shell character (one additional species used one shell character that was unique and not

categorized). The most common single distinguishing categories were sculpture (34 of 72 species, or 47%), shape (17 or 24%), and hinge (10 or 14%). Of the 13 species not citing any distinguishing shell characters, four were distinguished on the basis of habitat, whereas the other nine used anatomical characters. Of the categories, shell shape was most used (217 of 367 species, or 59%), followed by sculpture (205 or 56%), hinge (111 or 30%), size (94 or 26%), prodissoconch/umbones (78 or 21%), muscle scars/pallial lines and shell color (each 47 or 13%), inflation (43 or 12%), lunule/escutcheon (33 or 9%), thickness (32 or 9%), periostracum (27 or 7%), and ligament (18 or 5%).

Although the use of molecular data in molluscan systematics has seen a dramatic increase in the past decade (*e.g.*, Ponder and Lindberg 2008), such criteria are mainly utilized in bivalves at supraspecific levels. Only 9 of the 381 species (2%) were distinguished using molecular evidence, and all of these used molecular evidence in combination with morphological (usually shell) data. Two of the three commercial species were initially distinguished as molecular variants (Lam and Morton 2003, Richter *et al.* 2008), later confirmed by morphology.

Malacologists are generally not describing new species based on phylogenetic analyses. Only 12 of the 381 new species (3%) in seven publications are so supported. Of these, two studies coded morphological data alone (Cosel and Salas 2001 – 5 species; Simone 2009 – 2 species), and five coded molecular data alone (Lam and Morton 2003, Glover *et al.* 2004, Järnegren *et al.* 2007, Richter *et al.* 2008, Rodrigues *et al.* 2008). Although no studies coded both morphological and molecular characters, Cosel (2008a, 2008b) justified several new species of *Bathymodiolus* based on his morphological evidence and a generic-level molecular phylogeny presented earlier (Jones and Vrijenhoek 2006). Another two species were supported as new by a discriminant analysis (Kamanev 2002).

Taxonomic coverage

During the study period, malacologists have described new marine species from 51 of the *ca.* 100 living bivalve families (Table 1). The only taxa conspicuously missing from these descriptions are the Nuculoida and Trigonioida, the former being the more species-rich of the two. These data, however, are clearly highly dependent upon the research interests of active investigators. The greatest representation in this list is the Lucinidae (52 species), which reflects the productive research program of John Taylor and Emily Glover of The Natural History Museum (London) and their associates (Glover *et al.* 2004, Glover and Taylor 2007, Taylor and Glover 2005, Cosel in Taylor and Glover 2005, Cosel 2006). Condylocardiidae, with 33 species, ranks second, based on only three regional revisions by two investigators (Middelfart 2002a, 2002b, Coan 2003). Cardiidae, with 28

Table 1. Taxonomic coverage at the family level by new marine bivalve species described 2000-2009. Number following each taxonomic name is the number of new species described in that taxon during the period under discussion.

Protobranchia			11
Nuculoida		0	
Solemyoida		4	
Solemyidae	3		
Manzanellidae	1		
Nuculanoida		7	
Nuculanidae	1		
Yoldiidae	5		
Neilonellidae	1		
Autolamellibranchia			
Pteriomorphia			89
Arcoida		13	
Arcidae	7		
Glycymerididae	1		
Limopsidae	2		
Philobryidae	3		
Mytiloida		18	
Mytilidae	18		
Pterioida		3	
Ostreidae	1		
Gryphaeidae	2		
Limoida		16	
Limidae	16		
Pectinoida		39	
Pectinidae	15		
Propeamussiidae	14		
Spondylidae	10		
Heteroconchia			
Palaeoheterodonta			
Trigonioida		0	
Heterodonta			281
Carditoida		49	
Crassatellidae	2		
Astartidae	14		
Condylocardiidae	33		
Anomalodesmata		37	
Paralimyidae	1		
Pandoridae	1		
Clavagellidae	2		
Spheniopsidae	6		
Thraciidae	8		
Myochamidae	2		
Verticordiidae	3		
Poromyidae	6		
Cuspidariidae	8		
Veneroida		175	
Lucinidae	52		
Ungulinidae	2		
Thyasiridae	10		
Chamidae	1		
Galeommatidae	22		

Table 1. (Continued)

Veneroida (continued)		
Lasaeidae	1	
Leptonidae	1	
Kelliidae	1	
Montacutidae	2	
Chlamydoconchidae	1	
Kelliellidae	5	
Vesicomyidae	13	
Cyamiidae	3	
Cardiidae	28	
Veneridae	6	
Gaimardiidae	1	
Neoleptonidae	12	
Tellinidae	2	
Psammobiidae	2	
Semelidae	2	
Solenidae	8	
Myoida		20
Corbulidae	4	
Pholadidae	16	
Total	381	

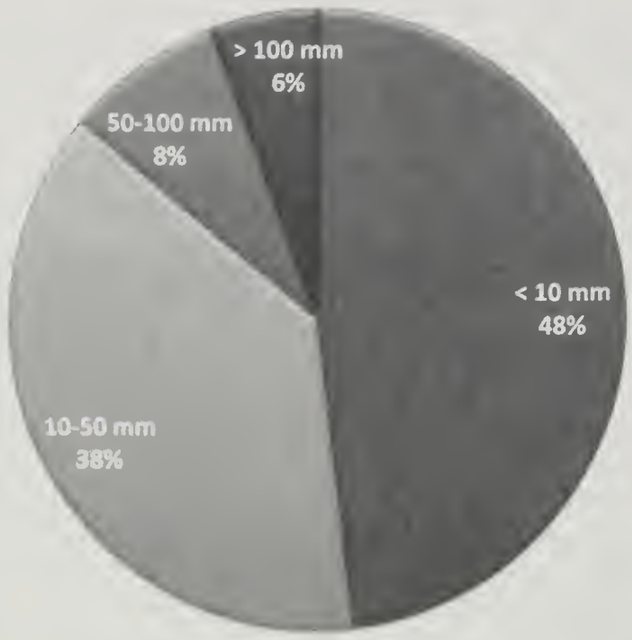

Figure 1. Body size (N = 381, ranging from 0.86 to 500 mm) of new marine bivalve species described during 2000-2009. More than half of the species are >1 cm in maximum dimension.

new species, ranks third from two groups of investigators (Hylleberg and Vidal in Vidal 2000, ter Poorten and Dekker 2002, Vidal 2003, Vidal and Kirkendale 2007). Another major representation is the superfamily Galeommatoidea, with all six families represented by a total of 28 new species from six separate sets of investigators (Simone 2001, 2008, Kamenev 2004b, Middelfart and Craig 2004, Middelfart 2005, Rotvit *et al.* 2007, Lützen and Takahashi 2003, Lützen and Nielsen 2005, Oliver and Holmes 2004).

Body size

Not everything new is small or cryptic. Malacologists are describing bivalves of a wide range of shell size, with the mean shell length (27.99 ± 50.82 mm *SD*) well within "naked eye" visibility, and maximum size for the species ranging from 0.86 mm (*Austrocardiella pouli* Middelfart, 2002; Condylocardiidae) to 500 mm (*Empressostrea kostini* Huber and Lorenz, 2007; Gryphaeidae). Although 185 species (48%) are <10 mm in maximum shell length, the remaining 52% is species of >10 mm, with 54 species (14%) >50 mm in maximum dimension (Fig. 1). So, although small species are certainly prominent among these new descriptions, malacologists are still describing new species of relatively large body size that have heretofore gone unnoticed.

Distribution

Malacologists are describing new species on a worldwide basis, with all oceanic basins represented: eastern Atlantic 60 (28 West Africa, 32 Europe/Mediterranean); western Atlantic 47 (25 North America/Caribbean, 22 South America); eastern Pacific 32 (19 North America/Caribbean, 13 South America); Indo-West Pacific 169 (including 36 New Caledonia); northwestern Pacific 36 (including 26 Japan); Indian Ocean 43; Antarctic 6; and Arctic 8. Many of these reflect the extensive research programs of Philippe Bouchet's colleagues (New Caledonia and other Indo-West Pacific locales), Rudo von Cosel (West Africa), and Luiz Simone and others (Brazil, now recognized as supporting a fauna more distinct from that of the northwestern Atlantic than previously thought). As for taxonomic coverage, this category is highly dependent on researchers and their interests.

Endemism is relative; that is, whether a species is "endemic" or not depends on the context or specific region under consideration. For example, a species can simultaneously be endemic to the Atlantic Ocean, the eastern United States, and Florida, but is not endemic to the Florida Keys if it is also known from Miami. With that qualification, only 2.6% (10 of 381 species) were actually stated as "endemic" in their original descriptions. Nevertheless, another 57% (219 of 381 species) were described as restricted to a particular geographic region (179 of 219 species, or 82%), a particular specialized habitat (12 of 219 species, or 5.5%), or both (28 of 219 species, or 13%). Admittedly, some of these species might not truly be restricted or endemic, but are so far only known from a single place (usually the type locality), such as the Edison Seamount (*e.g.*, *Bathymodiolus anteumbonatus* Cosel, 2008a) or the Argentine Basin (*e.g.*, *Neolepton profundorum* Allen, 2004); such characterizations might be limited by the fact that we

have not sampled in that location often or even more than once. Other such cases are from more widely sampled areas, such as Brazil (*e.g.*, *Solemya notialis* Simone, 2009), where the faunas are relatively well known but perhaps not adequately revised taxonomically. Also included here are species with highly specialized habitat, such as methane seeps (*e.g.*, *Thyasira methanophila* Oliver and Sellanes, 2005), submarine volcanos (*e.g.*, *Gigantidas gladius* Cosel and Marshall, 2003), submarine caves (*e.g.*, *Empressostrea kostini* Huber and Lorenz, 2007), and reducing sediments (*e.g.*, *Lucinoma myriamae* Cosel, 2006), again areas which likely suffer from minimal sampling effort. Still another category here are bivalves that are commensal with other invertebrates, such as sponges (*e.g.*, *Troglodytoconcha carpentariensis* Middelfart, 2005), crabs (*e.g.*, *Arthritica japonica* Lützen and Takahashi, 2003), and holothurians (*e.g.*, *Austrodevonia sharnae* Middelfart and Craig, 2004). Another 152 species (40%) in the dataset are not restricted in habitat or in distribution within the context of the original author(s).

This dataset also includes new species from a wide range of water depths. Okutani and Soh (2005: 28) stated that "bathymetrical difference is another important clue for speciation," and several authors included in this survey (Allen 2000, 2007, Sasaki and Haga 2007) stated depth criteria in support of new species (*e.g.*, the new species in question is the first in a given group from the intertidal zone or from abyssal depths). Minimum recorded depth shows a mean of 444.1 ± 841.41 m (N = 327 m, ranging 0-7,299 m, with intertidal scored as 0), with 138 species (of 327 or 42%) from >100 m (Fig. 2). Maximum recorded depth showed a mean of 733.14 ± 884.46 m (N = 324 spp., ranging 0-7,333 m, with intertidal scored as 0), but included substantially more species (222 of 327 species, or 68%) from >100 m. The range of depths recorded for new species (*i.e.*, the difference between maximum and minimum recorded depth; scored for 324 spp.) ranges from 0-6,795 m, with 146 species (of 324 or 45%) from >100 m and 21 species (of 324 or 6%) from >1,000 m. So, we can reasonably summarize that we are currently describing many new species from deep water, another inadequately explored habitat, but that new shallow-water species also continue to be discovered.

Summary and discussion

What do these 381 new species descriptions reflect about speciation? At first glance, not much. Malacologists are clearly still exploring and continuing to document undiscovered diversity on a regular basis. So, these new species are not newly isolated species, but rather of the results of intensified collecting (*e.g.*, MUSORSTOM Project, http://www.mnhn.fr/musorstom/index.html). This small sample of the recent literature includes the first lucinid from hydrothermal vents (*Bathyaustriella thionipta* Glover

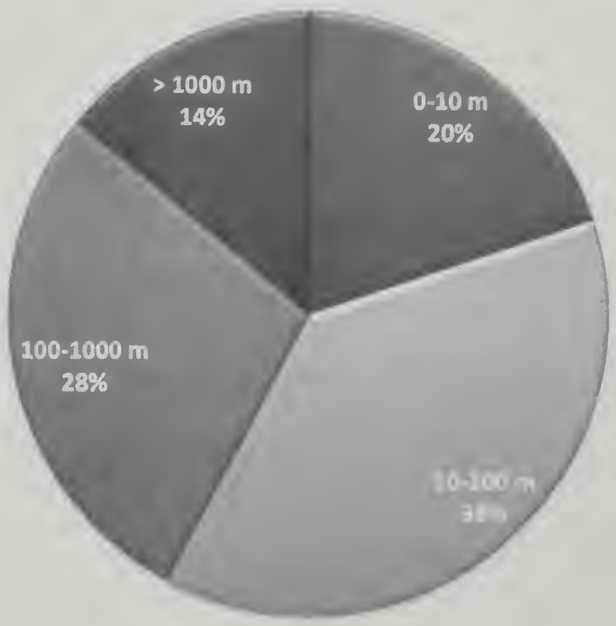

Figure 2. Minimum recorded depth (N = 327 m, ranging from 0 to 7,299 m, with intertidal scored as 0) in new marine bivalve species described during 2000-2009. 42% of the species inhabit deep water (>100 m).

et al., 2004), the first deep-water neoleptonid (*Neolepton profundorum* Allen, 2000), the first abyssal *Epilepton* (*E. elpis* Allen, 2007), the first galeommatoidean associated with Australian holothurians (*Austrodevonia sharnae* Middelfart and Craig, 2004), the smallest known bathymodioline (*Bathymodiolus taiwanensis* Cosel, 2008b), the second largest living mytilid (*Gigantidas gladius* Cosel and Marshall, 2003), and the first ostreid to be described genetically (*Crassostrea hongkongensis* Lam and Morton, 2003). This ten-year record includes large and small species over a wide taxonomic and geographic range. Their descriptions rely heavily upon shell morphology (most often sculpture, shape, and hinge), but include substantial contributions from soft anatomy and minor contributions from molecules and phylogenetic analyses. Amano and Lutaenko (2004: 19) noted that their new species, *Limopsis oliveri*, has no fossil record and "might have arisen very recently"; this statement could likely be supposed of many of these recently described species.

In the apparent paucity of allopatric species barriers in the marine realm, one important key to apparently sympatric speciation is, according to this study, specialization. Marine gastropods illustrate this well, with their many dietary and developmental (especially nonplanktonic) strategies (reviewed by Krug 2011). Because the vast majority of bivalves are broadcast-spawning filter feeders, such cases are rare (although not unheard of, see below). However, there are other ways that marine bivalves can specialize, and a number of them are present in this dataset. First and most generally, the high

percentages of deep-water and otherwise restricted bivalve species suggest that ecological or physiological limits can set up barriers to gene flow. Jones *et al.* (2005) convincingly provided molecular phylogenetic evidence for multiple invasions of deep-water hydrocarbon seep and hydrothermal vent habitats by species of Bathymodiolinae (Mytilidae), showing the effectiveness of bathymetric specialization for the radiation of this subfamily.

In one of the few examples of dietary specialization in bivalves, Järnegren *et al.* (2007) showed their new species of file clam, *Acesta oophaga* Järnegren, Schander, and Young, 2007, to be a highly specialized member of the cold seep community in the northern Gulf of Mexico. Not only is it restricted in habitat, it is unique among bivalves, and so far among all marine animals, in its specialized method of feeding. This species is always found byssally attached to the sabellid polychaete *Lamellibranchia luymesi* and ingests the eggs ejected by the tubeworm, capitalizing on the chemosynthetic abilities of its prey to survive in a reducing environment without the cost of maintaining symbionts of its own. Prior to this study and the direct observations by manned submersible that it included, *A. oophaga* was misidentified in collections as *A. bullisi* Vokes, 1963 or *A. excavata* (Fabricius, 1779), two species found in the general distributional range of *A. oophaga*, but neither of which are associated with either seeps or tubeworms. Because exploration of the deep sea, and discovery of additional new deep-sea species, are strongly represented in this dataset and can be expected to continue in the immediate future, we can expect to see additional research along the lines of these last two examples, which provide at least circumstantial support for specialization as a component of possible mechanisms of bivalve speciation.

Another type of specialization is that of host associations. In addition to the bivalve species mentioned above that are commensal with other invertebrates, Richter *et al.* (2008) showed that *Tridacna* spp. (including the new species *T. costata* Roa-Quiaoit, Kochzius, Jantzen, Zibdah, and Richter, in Richter *et al.*, 2008), like some species of coral, differ in the various strains or clades of zooxanthellae (*Symbiodinium*) found in their mantle tissues and on which they physiologically depend. These differences in symbiont composition are correlated with habitat, with those harboring clade A symbionts being found on reef flats, and those hosting both clades A and B inhabiting a wider depth range, but importantly, able to invade deeper fore reefs. Such differences have apparently prompted adaptation among *Tridacna* spp. to particular light regimes associated with their individual complements of phototrophic symbionts. Such a case might have resulted from a cline within a continuous population (as discussed, *e.g.*, by Valentine and Jablonski 1983).

Species complexes

Although not clearly evident from recent new species descriptions, examples suggesting ongoing speciation in the form of cryptic species complexes can be found in the marine bivalve record. Species complexes are either (1) groups of closely related nominal species whose morphological boundaries are difficult to define (AKA sibling, incipient, or cryptic species; Knowlton 1993, Gardner 1994, 1996), or (2) highly variable species that have been revealed by molecular or other analyses to be composed of more than one species, but whose morphological boundaries remain elusive (Goffredi *et al.* 2003, Lee and Ó Foighil 2004). Here are brief descriptions of seven examples that have appeared in recent literature:

(1) The species *Mytilus edulis* Linnaeus, 1758 [native to northeastern and northwestern Atlantic], *M. galloprovincialis* Lamarck, 1819 [northeastern Atlantic], *M. trossulus* Gould, 1850 [northeastern and northwestern Pacific, northeastern and northwestern Atlantic], *M. californianus* Conrad, 1837 [northeastern Pacific], and *M. chilensis* (Hupé, 1854) [southeastern Pacific] comprise a species complex of superficially similar "blue mussels" in temperate intertidal habitats around the globe. They byssally attach to hard substrata and are broadcast spawners. They have been harvested for food by humans for at least the past 12,000 years (Erlandson *et al.* 2008). Some of these species are additionally raised in aquaculture and are (importantly) anthropogenically transported alive from market to market, further blurring species boundaries. For example, two species pairs (*M. edulis-galloprovincialis* in southwestern Europe and *M. edulis-trossulus* in Scandinavia and Atlantic Canada) are known to hybridize and have become models for studies of hybrid-zone structure, involving considerations such as genetic identification methods, local adaptation, hybrid fitness, asynchronous spawning, gamete recognition, and fertilization preference (*e.g.*, Gardner 1994, 1996, Rawson *et al.* 1996, Comesaña *et al.* 1999, Bierne *et al.* 2002a, 2002b, Riginos and Cunnngham 2005, Toro *et al.* 2005, Braby and Somero 2006). Although their genotypes are clearly identified, little morphological resolution is available and they comprise a classic example of a species complex. No resolution of the taxonomic issues, either through synonymy or erection of new species, has been attempted.

(2) The small-bodied pearl oysters of the world—*Pinctada imbricata* Röding, 1798 [western Atlantic], *P. fucata* (Gould, 1850) [Indo-West Pacific], *P. martensii* (Dunker, 1857) [Japan], *P. radiata* (Leach, 1814) [Persian Gulf]—are widely raised in aquaculture or harvested for use in pearl culture. These names are historically regional, and in at least one case, political, with strong ties to the commercial pearl industry; Japanese perliculturists prefer to consider their pearl oyster, which they call *P. martensii*, endemic to Japan.

Biologically, however, according to recent molecular data and phylogenetic analyses (Masaoka and Kobayashi 2002, 2003, 2005a, 2005b, Yu and Chu 2006, Tëmkin 2007), all seem to belong to one circumglobal species complex "characterized by substantial intraspecific variation largely due to color and size differences" (Tëmkin 2007: 318). No morphological characters have been found to dispute the molecular results and the four species have been synonymized under the senior synonym *P. imbricata*.

(3) Members of the galeommatoidean genus *Lasaea* [*e.g.*, *L. adansoni* (Gmelin, 1791), *L. rubra* (Montagu, 1803), *L. maoria* (Powell, 1933), *L. subviridis* Dall, 1899, and others] inhabit intertidal turf-algal and rock-crevice habitats worldwide. Unusually for marine bivalves, they are hermaphroditic brooders with direct development. Their complex genetics includes instances of polyploidy and within-island cladogenesis associated with their specialized larval development, and proposed dispersal/colonization events are equally complex (Ó Foighil and Smith 1996, Ó Foighil and Jozefowicz 1999, Ó Foighil and Thiriot-Quiévreux 1999, Park and Ó Foighil 2000, Ó Foighil *et al.* 2001). Although hybridization apparently does not occur, sympatric asexual clones have been detected (Crisp and Standen 1988, Ó Foighil and Smith 1995) that "represent highly divergent phylogenetic lineages" (Ó Foighil *et al.* 2001). Morphological differences within this species complex are unresolved and all species names continue to be used as distinct.

(4) Small mytilids of the genus *Brachidontes* are byssate on shallow-water rocks and have planktonic larvae. They are tolerant of high salinities and temperatures, and show high levels of morphological variability. A molecular phylogeny of the species *B. variabilis* (Krauss, 1848) from the Mediterranean Sea, Red Sea [from these last two often as *B. pharaonis* (P. Fischer, 1870)], Indian Ocean, and western Pacific indicated three cryptic species from these locations, diverging in the Miocene Epoch, approx. 6-11 million years ago (Terranova *et al.* 2007). Vicariance events during Pleistocene glaciations and the opening of the Red Sea were proposed as the mechanisms underlying speciation in this complex although morphological characters supporting this separation are as yet unclear. A similar study of *B. exustus* (Linnaeus, 1758) in the western Atlantic revealed a species complex of five as-yet-unnamed distinct genotypes in peninsular Florida and the Caribbean alone, likely driven in this case by post-recruitment ecological barriers (Lee and Ó Foighil 2004, 2005).

(5) The file clams *Limatula ovalis* Thiele, 1912 and *L. pygmaea* (Philippi, 1845) inhabit deep waters of the Antarctic or sub-Antarctic regions, respectively, on soft bottom in cobweb-like nests of their own construction. Shells of *Limatula* spp. are well-known to be highly conservative (*i.e.*, closely similar), making shell characters difficult to use for species identification (independent of locality) or phylogenetic reconstruction. A recent molecular phylogeny (Page 2002, Page and Linse 2002) supports their divergence less than 20 million years ago. In this case, the Antarctic Polar Front has been proposed as a temperature barrier maintaining the two species.

(6) Vesicomyid clams are dominant organisms in the world's chemosynthetic-based deep-sea communities. Species-level variation in the ability to uptake product from sulfide-metabolizing symbionts suggests that physiological specialization is at work in maintaining sympatric species (Goffredi and Barry 2002). In another study involving molecular and morphometric analyses (Goffredi *et al.* 2003), five lineages—*Vesicomya pacifica* (Dall, 1891), *V. lepta* (Dall, 1886), and three undescribed species of *Vesicomya*—were identified. All five species are broadcast spawners, which are nevertheless segregated by depth and thus presumably diverged and are maintained by bathymetric and substratum factors exerted at the recruitment level. Although two existing species names have been applied to two of these lineages, morphological criteria distinguishing these plus the three undescribed species remain unconfirmed.

(7) The western Atlantic oyster *Crassostrea virginica* (Gmelin, 1791) ranges in hyposaline estuaries from eastern Canada to the Gulf of Mexico, and is well-known to include physiological "races" (Ahmed 1975, Dittman *et al.* 1998). Morphological evidence first provided in the 1950s (Loosanoff and Nomejko 1951) is complicated by the fact that morphological characters are extremely phenotypically plastic in Ostreidae, a taxonomic difficulty among bivalves that is certainly not unique to this family. Indeed, *C. hongkongensis* Lam and Morton, 2003 went unrecognized in part because morphology is so variable among oysters. Morphological data for *C. virginica* have since been supplemented by molecular data (*e.g.*, Peterson 2006, Varney *et al.* 2009) that confirm clines even in small parts of the geographic range, yet accepted nomenclature continues to recognize a single, variable species. This case is complicated by the fact that *C. virginica* is widely cultivated in aquaculture in the region for human consumption. Other species of oysters (*e.g.*, *Ostrea edulis* Linnaeus, 1758 of Europe; Ahmed 1975) show similar patterns.

Table 2 summarizes these seven examples, showing that species complexes can be either revealed or resolved by molecular analyses, even in the absence of morphological evidence. In two of these species complexes (*Brachidontes* and *Vesicomya*), incipient speciation is clearly suggested; alternatively, we simply could be at a stage of correcting overly conservative taxonomy. More importantly, this kind of research on species complexes has revealed apparent barriers to gene flow in the marine realm that are physiological (sympatric, *e.g.*, temperature in *Limatula*, bathymetry in

Table 2. Species complexes discussed herein, with their initial level of variation, support from molecular and morphological data, presumed reproductive barriers, the beginning and ending numbers of species, and whether molecular data revealed or resolved species complex issues. See text for pertinent references.

Taxa	Variation	Molecules	Morphology	Barrier(s)	Species	Outcome
Mytilus	low	yes	no	???	5 → (5)	revealed
Pinctada	low	no	no	none	4 → 1	resolved
Lasaea	low	yes	no	isolated "islands"	n → ?	revealed
Brachidontes	high	yes	no	Miocene vicariance or salinity/ temperature	1 → 3-4	revealed
Limatula	low	yes	yes	temperature	2 → 2	resolved
Vesicomya	low	yes	no	bathymetry, substratum	2 → 5	revealed
Crassostrea	high	yes	yes	???	1 → ?	revealed

Vesicomya) or physical (allopatric, *e.g.*, Miocene vicariance events in *Brachidontes*, isolated "island" habitats in *Lasaea*), some of which can be, nevertheless, broken down by anthropogenic transport (*e.g.*, resulting in hybridization in *Mytilus*).

Phylogenetic analyses

Phylogenetic analyses, especially at low (generic or familial) taxonomic levels, can show clade patterns that reveal radiation and suggest the innovations that facilitated that radiation. One must look for either of two patterns: (1) speciose clades as part of strongly disparately sized sister taxa (here size indicating numbers of species/clade, *i.e.*, indicating radiation of the more species-rich sister) coupled with the synapomorphies (*i.e.*, the recognized evolutionary innovations) of the more species-rich sister, or (2) unresolved polytomies that might indicate unacknowledged species complexes or rapid ongoing speciation. The following text provides one example of each pattern.

When numbers of recognized species per superfamily are superimposed on a bivalve tree (Fig. 3), four sister pairs are revealed showing highly unequal species per sister and recognized synapomorphies suggesting innovations: (1) Unionoidea (688 spp., all freshwater) and Trigonioidea (5 spp.) suggest the glochidium (*i.e.*, the specialized unionoidean larval type that depends upon a fish host to complete metamorphosis) as the innovation promoting unionoidean radiation; (2) Lucinoidea (500 spp.) and Galeommatoidea (30 spp.) + Pholadoidea (170 spp.) suggest commensalism with sulfide-oxidizing bacteria and mucus-tube feeding that allow habitation of a reducing environment as innovations of the more species-rich sister; (3) Tellinoidea (645 spp.) and Chamoidea (70 spp.) + Cardioidea (255 spp.) suggest that the cruciform muscle and very long siphons are innovations of Tellinoidea that allowed very deep burrowing in soft sediments; and (4) Veneroidea (820 spp.) and Arcticoidea (1 spp.) suggest that the aortic bulb (a muscular, spongy structure on the ventral side of the posterior aorta, which prevents rupture of the heart when the siphons and foot retract suddenly) is an innovation that facilitates rapid retraction and valve closure in siphonate veneroideans. According to the dates of first occurrence in the fossil record, these innovations occurred in the Triassic (1), Ordovician (2), and Jurassic (3, 4), in strong congruence with the cladogram topology.

The molecular phylogeny of Lucinoidea presented by Williams *et al.* (2004) shows the family Lucinidae as a strongly supported polytomy, with one of its clades, called "Lucinid clade B + *Phacoides*," also as a strongly supported polytomy. This tree was generated by molecular data alone, so morphological synapomorphies are difficult to identify; however, the authors did accept that some characters that were previously considered diagnostic for one group or another were homoplastic according to this tree. All lucinids to date are known to harbor ctenidial chemosynthetic bacteria within bacteriocytes. Chemosymbiosis allows lucinids to inhabit oligotrophic environments, which is not unique, but this specialized location for the symbionts differs from that of other symbiont-bearing bivalves, and might be a more recent novelty than can be estimated from the fossil record. Given the well-studied status of this family, the polytomies in this analysis likely do not indicate unrecognized species complexes, but rather possible parts of the cladogram with taxa undergoing rapid evolutionary change. This suggests a focus for fruitful future research.

CONCLUSIONS

The three types of data from the recent literature presented here—new species descriptions, species complexes, and phylogenies at low taxonomic levels—provide insight into possible mechanisms of speciation occurring in recent marine bivalves. Specialization is revealed as one of the more important factors facilitating speciation in bivalves in the seemingly homogenous sea. Ecological or physiological specialization can create effective barriers between sympatric species (a documented phenomenon in animals such as fish, aphids, and gastropods, *e.g.*, Hollander *et al.* 2005), and is illustrated here by bathymodioline mussels invading deep-water

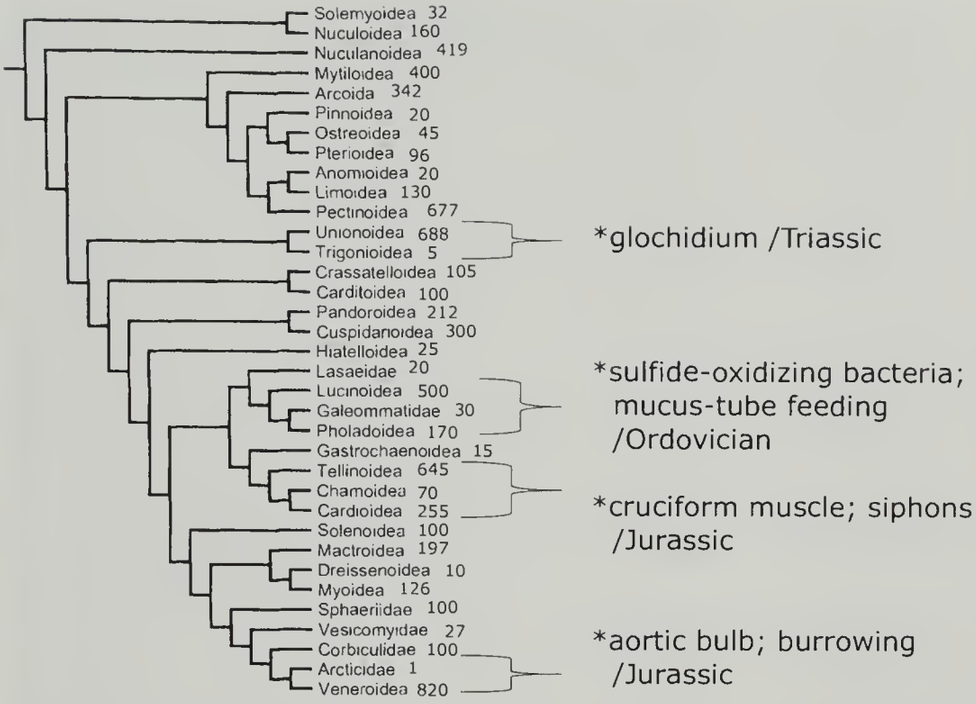

Figure 3. The numbers of recognized species per Recent bivalve superfamily (from Mikkelsen and Bieler 2008) superimposed on the morphological + molecular bivalve cladogram by Giribet and Wheeler (2002: fig. 11). Four disparately sized sister pairs are recognized (Unionoidea-Trigonoidea; Lucinoidea-Galeommaoidea + Pholadoidea; Tellinoidea-Chamoidea + Cardioidea; Veneroidea-Arcticoidea), with their synapomorphies (*i.e.*, innovations that drove radiation of the more species-rich sister) and dates of first occurrence from the fossil record.

habitats, an egg-eating *Acesta,* multiple strains of zooxanthellae segregating *Tridacna* spp. by depth, the Antarctic Polar Front as a temperature barrier for *Limatula* spp., larval vesicomyid clams responding to bathymetric and substratum factors, and physiological "races" of oysters. This analysis also identified two probable cases of allopatric speciation: direct-developing *Lasaea* spp. in isolated turf or crevice "islands," and *Brachidontes* diverging in response to Miocene vicariance events. It does not follow, however, that species-rich clades are necessarily more "specialized" bivalves overall; few bivalve experts would call members of the Veneroidea "specialized," yet the aortic bulb apparently allowed them a physiological advantage over other members of their ancestral clade. Together these data defeat the concept of a Marine Speciation Paradox in bivalves—speciation clues are merely more subtle than those in terrestrial systems and most often act at the physiological, rather than physical, level.

One factor that could not be traced by this analysis but which could impact the process (or at least the rate) of speciation in bivalves is life span. Certainly, researchers use the fruit fly (*Drosophila melanogaster*) as a model in evolutionary studies in part because its extremely short life span (30 days or less) allows one to observe rapid changes. One of the largest-bodied new species tabulated here is *Neopycnodonte zibrowii* Gofas, Salas, and Taviani, in Wisshak *et al.*, 2009; the authors claimed that through radiocarbon dating, they determined that this bivalve can reach >500 years of age (at a maximum size of 300 mm). Species that are raised in aquaculture have generally well-understood life spans; others have been analyzed via the growth increments in their shells. A few examples are: *Donax* spp., 1 year (Buttemer *et al.* 2010), *Argopecten gibbus* (Linnaeus, 1758), 2 years (Roe *et al.* 1971), *Pinctada margaritifera* (Linnaeus, 1758), 6 years (in culture; Landman *et al.* 2001), *Mytilus edulis,* 18 years (Sukhotin *et al.* 2007), *Mya arenaria* Linnaeus, 1758, 28 years, *Spisula solidissima* (Dillwyn, 1817), 30 years, *Mercenaria mercenaria* (Linnaeus, 1758), 75 years (the last three summarized by Jones 1989), *Tridacna gigas* (Linnaeus, 1758), 100 years (Comfort 1957), *Panopea generosa* Gould, 1850, 120 years (B. Black, http://people.oregonstate.edu/~Blackbry/reserach.htm), and *Arctica islandica* (Linnaeus, 1767), 410 years (Wanamaker *et al.* 2008). Does a long life span impede speciation in any way (*e.g.*, long-lived Arcticoidea with 1 species versus shorter-lived Veneroidea with 820 species)? Additional consideration of this topic is warranted.

To further interpret this record, we need (1) a robust phylogenetic framework for Bivalvia [currently being pursued by the BivAToL Project (www.bivatol.org) and other groups], (2) additional molecular work on taxa with "difficult" (*i.e.*, variable or homogenous) morphology, in search of unrecognized species complexes, especially where suggested by wide geographical or depth distributions [two such examples are *Hiatella arctica* (Linnaeus, 1767), which ranges from Greenland to Mexico, and worldwide species of *Perna* that as commercial "green mussels" have been anthropogenically introduced to many non-native locations], and (3) additional taxon-rich genus-level phylogenies in which to identify novelties and rapidly evolving clades.

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Appendix. New marine bivalve species and subspecies (arranged alphabetically by family) described during the years 2000-2009. Tabulated data are taken from the original descriptions. Y, yes; N, no; na, not applicable or none listed; see footnotes for other abbreviations.

Species	Family	Zone[1]	Dep[2]	Size[3]	Live[4]	Anat[5]	Mol[6]	Anl[7]	Res[8]	Source[9]
Acar marsupialis Oliver and Holmes, 2004	Arcidae	IO	17	2.58	N	N	N	N	Y	na
Acar transmar Simone, 2009b	Arcidae	WA	8	5	Y	Yd	N	P	N	na
Arca koumaci Lutaenko and Maestrati, 2007	Arcidae	IP	57	6.1	N	N	N	N	N	NC
Barbatia diphaeonotus Oliver and Holmes, 2004	Arcidae	IO	18	6.55	Y	N	N	N	N	na
Barbatia pyrrhotus Oliver and Holmes, 2004	Arcidae	IO	18	4.9	Y	N	N	N	N	na
Samacar (Pseudoporterius) aleutica Kamanev, 2007	Arcidae	EP	168	18	N	N	N	N	Y	NC
Samacar (Samacar) kurilensis Kamanev, 2007	Arcidae	NWP	368	20.9	Y	Y	N	N	Y	na
Astarte anholti Petersen, 2001	Astartidae	EA	22	24.8	N	N	N	N	Y	NC
Astarte belti Petersen, 2001	Astartidae	EA	15	35	N	N	N	N	Y	NC
Astarte bornholmi Petersen, 2001	Astartidae	EA	93	22.7	Y	N	N	N	Y	NC
Astarte elonga Petersen, 2001	Astartidae	AC	na	23.5	N	N	N	N	Y	NC
Astarte falsteri Petersen, 2001	Astartidae	EA	70	23	N	N	N	N	Y	NC
Astarte fjordi Petersen, 2001	Astartidae	EA	24	19	N	N	N	N	Y	NC
Astarte jenseni Petersen, 2001	Astartidae	EA	30	36.3	N	N	N	N	Y	NC
Astarte klinti Petersen, 2001	Astartidae	EA	38	15.5	N	N	N	N	Y	NC
Astarte moerchi Petersen, 2001	Astartidae	AC	na	37.9	N	N	N	N	Y	NC
Astarte neocrassa Petersen, 2001	Astartidae	AC	na	27.2	N	N	N	N	Y	NC
Astarte nordi Petersen, 2001	Astartidae	EA	56	33.5	N	N	N	N	Y	NC
Astarte nuuki Petersen, 2001	Astartidae	AC	na	38	N	N	N	N	Y	NC
Astarte silki Petersen, 2001	Astartidae	EA	93	27.5	Y	N	N	N	Y	NC
Astarte vaigati Petersen, 2001	Astartidae	AC	na	30	N	N	N	N	Y	NC
Acrosterigma capricorne Vidal and Kirkendale, 2007	Cardiidae	IP	1350	58.1	Y	N	N	N	Y	na
Acrosterigma suduirauti Vidal and ter Poorten, 2007	Cardiidae	IP	150	37.8	N	N	N	N	Y	na
Cardium maxicostatum ter Poorten, 2007	Cardiidae	EA	28	130	N	N	N	N	N	na
Ctenocardia fijianum Vidal and Kirkendale, 2007	Cardiidae	IP	34	12	N	N	N	N	Y	na
Ctenocardia gustavi Vidal and Kirkendale, 2007	Cardiidae	IP	54	20	Y	N	N	N	N	na
Ctenocardia subfestivum Vidal and Kirkendale, 2007	Cardiidae	IP, NWP	400	10.3	Y	N	N	N	N	na
Fragum grasi ter Poorten, 2009	Cardiidae	IP	21	8	Y	N	N	N	N	NC
Frigidocardium helios ter Poorten and Poutiers in ter Poorten, 2009	Cardiidae	IP	102	9.5	Y	N	N	N	N	NC
Frigidocardium iris Huber and ter Poorten, 2007	Cardiidae	IP	200	28.3	N	N	N	N	N	na
Frigidocardium sancticaroli ter Porten and Poutiers in ter Poorten, 2009	Cardiidae	IP	210	11.3	Y	N	N	N	N	NC
Frigidocardium valdentatum Poutiers, 2006	Cardiidae	IP	460	27.5	N	N	N	N	N	NC

Appendix. (Continued)

Species	Family	Zone[1]	Dep[2]	Size[3]	Live[4]	Anat[5]	Mol[6]	Anl[7]	Res[8]	Source[9]
Fulvia colorata Vidal and Kirkendale, 2007	Cardiidae	IP	82	16.4	Y	Y	N	N	N	na
Fulvia imperfecta Vidal and Kirkendale, 2007	Cardiidae	IP	53	10.9	N	N	N	N	N	na
Fulvia subquadrata Vidal and Kirkendale, 2007	Cardiidae	IP	286	17.2	N	N	N	N	N	na
Fulvia vepris Vidal and Kirkendale, 2007	Cardiidae	IP	na	15.8	N	N	N	N	Y	na
Lunulicardia orlini Mienis, 2009	Cardiidae	EA	49	44.59	N	N	N	N	N	na
Lyrocardium anaxium dekkeri Mienis, 2009	Cardiidae	EA	92	55.62	Y	Y	N	N	N	na
Microcardium trapezoidale Poutiers, 2006	Cardiidae	IP	806	20	Y	N	N	N	N	NC
Microcardium velatum ter Poorten and Poutiers in ter Poorten, 2009	Cardiidae	IP	356	16	Y	N	N	N	Y	NC
Parvicardium carrozzai Van Aartsen and Goud, 2001	Cardiidae	EA	300	9	N	N	N	N	N	na
Pseudofulvia arago Vidal and Kirkendale, 2007	Cardiidae	IP	107	27	Y	Yd	N	N	Y	na
Pseudofulvia caledonica Vidal and Kirkendale, 2007	Cardiidae	IP	446	13.4	Y	Yd	N	N	N	na
Tridacna costata Roa-Quiaoit, Kochzius, Jantzen, Zibdah, and Richter in Richter *et al.*, 2008	Cardiidae	IO	2	320	Y	Yd	Y	P	Y	C
Trifaricardium morrisoni ter Poorten and Huber, 2007	Cardiidae	IO	300	11.9	N	N	N	N	N	na
Vasticardium lomboke Vidal, 2003	Cardiidae	IP	sh	28.9	N	N	N	N	Y	na
Vasticardium subassimile Vidal, 2003	Cardiidae	IP	na	65.4	N	N	N	N	N	na
Vepricardium albohamatum Hylleberg and Vidal in Vidal, 2000	Cardiidae	IP	na	44.2	N	N	N	N	Y	R
Vepricardium vidali ter Poorten and Dekker, 2002	Cardiidae	IO	sh	54.3	Y	Y	N	N	Y	na
Chama cerion Matsukuma, Paulay, and Hamada, 2003	Chamidae	IP,IO, NWP	30	25.9	Y	N	N	N	N	na
Chlamydoconcha avalvis Simone, 2008	Chlamydoconchidae	WA	6	15	Y	Yd	N	N	Y	na
Bryopa aligamenta Morton, 2005	Clavagellidae	NWP	na	20	Y	Y	N	N	Y	na
Dianadema mascarensis Oliver and Holmes, 2004	Clavagellidae	IO	17	9.48	N	N	N	N	Y, H	na
Austrocardiella pouli Middelfart, 2002a	Condylocardiidae	IO	150	0.86	N	N	N	N	E	R
Benthocardiella burtonae Middelfart, 2002a	Condylocardiidae	IP	73	1.42	N	N	N	N	Y	R
Benthocardiella darwinensis Middelfart, 2002a	Condylocardiidae	IP	na	1.21	N	N	N	N	Y	R
Carditella marieta Coan, 2003	Condylocardiidae	EP	46	2	N	N	N	N	N	R
Condylocardia cometa Middelfart, 2002a	Condylocardiidae	IP	131	1.35	N	N	N	N	Y	R
Condylocardia elongata Coan, 2003	Condylocardiidae	EP	30	2.4	N	N	N	N	Y	R
Condylocardia fernandina Coan, 2003	Condylocardiidae	EP	110	2.1	N	N	N	N	Y	R

Appendix. (Continued)

Species	Family	Zone[1]	Dep[2]	Size[3]	Live[4]	Anat[5]	Mol[6]	Anl[7]	Res[8]	Source[9]
Condylocardia galapagana Coan, 2003	Condylocardiidae	EP	228	2.6	N	N	N	N	N	R
Condylocardia geigeri Coan, 2003	Condylocardiidae	EP	124	1.9	N	N	N	N	Y	R
Condylocardia kaiserae Coan, 2003	Condylocardiidae	EP	274	3.1	N	N	N	N	N	R
Condylocardia koosae Coan, 2003	Condylocardiidae	EP	274	2.2	N	N	N	N	Y	R
Condylocardia sparsa Coan, 2003	Condylocardiidae	EP	35	2.2	N	N	N	N	N	R
Condylocuna anneae Middelfart, 2002a	Condylocardiidae	IP	201	1.15	N	N	N	N	Y	R
Condylocuna jimbecki Middelfart, 2002a	Condylocardiidae	IP	201	0.98	N	N	N	N	Y	R
Condylocuna tricosa Middelfart, 2002a	Condylocardiidae	IP	103	0.88	N	N	N	N	N	R
Crassacuna crassisculpta Middelfart, 2002b	Condylocardiidae	IP	124	2.13	N	N	N	N	N	R
Cuna deltoides Middelfart, 2002b	Condylocardiidae	IP	81	1	N	N	N	N	N	R
Cuna libbyae Middelfart, 2002b	Condylocardiidae	IP	1465	1.9	N	N	N	N	N	R
Cuna microcentrica Middelfart, 2002b	Condylocardiidae	IP	81	1.3	N	N	N	N	N	R
Cuna navicula Middelfart, 2002b	Condylocardiidae	IP	128	1.8	N	N	N	N	N	R
Cuna ranus Middelfart, 2002b	Condylocardiidae	IP	201	2.7	N	N	N	N	N	R
Isodontocardia microcardia Middelfart, 2002a	Condylocardiidae	IP	65	1.58	N	N	N	N	N	R
Mimicuna cuniformis Middelfart, 2002b	Condylocardiidae	IP	31	1.08	N	N	N	N	Y	R
Warrana brucemarshalli Middelfart, 2002b	Condylocardiidae	IP	36	2.13	N	N	N	N	N	R
Warrana flexuosa Middelfart, 2002b	Condylocardiidae	IP	150	1.83	N	N	N	N	N	R
Warrana lunata Middelfart, 2002b	Condylocardiidae	IP	294	2.82	N	N	N	N	N	R
Warrana pauciconcentrica Middelfart, 2002b	Condylocardiidae	IP	85	1.01	N	N	N	N	N	R
Warrana pellucida Middelfart, 2002b	Condylocardiidae	IP	256	2.07	N	N	N	N	N	R
Warrana punicea Middelfart, 2002b	Condylocardiidae	IP	155	1.47	N	N	N	N	N	R
Warrana triangulata Middelfart, 2002b	Condylocardiidae	IP	23	0.9	N	N	N	N	Y	R
Warrana westralis Middelfart, 2002b	Condylocardiidae	IP	158	1.26	N	N	N	N	N	R
Westaustrocuna albanyensis Middelfart, 2002b	Condylocardiidae	IP	146	1.05	N	N	N	N	N	R
Westaustrocuna keegani Middelfart, 2002b	Condylocardiidae	IP	155	1.14	N	N	N	N	N	R
Corbula colimensis Coan, 2002b	Corbulidae	EP	112	14	N	N	N	N	N	na
Corbula grovesi Coan, 2002b	Corbulidae	EP	732	11	N	N	N	N	Y	na
Corbula otra Coan, 2002b	Corbulidae	EP	55	26.1	N	N	N	N	N	na
Corbula tarasconii Arruda, Domaneschi, Francisco, and de Barros, 2007	Corbulidae	WA	65	7.2	N	N	N	N	N	na
Crassatina rikai Lamprell, 2003	Crassatellidae	IP	300	14.7	N	N	N	N	Y	R
Crassatina suduirauti Lamprell, 2003	Crassatellidae	IP	180	26	N	N	N	N	N	R
Cuspidaria altenai Knudsen, 2005	Cuspidariidae	WA	300	12.4	N	N	N	N	Y	NC
Cuspidaria luymesi Knudsen, 2005	Cuspidariidae	WA	94	15.9	Y	Y	N	N	Y	NC
Plectodon lepidus Marshall, 2002	Cuspidariidae	IP	83	6.1	Y	N	N	N	N	na
Plectodon pruniosus Marshall, 2002	Cuspidariidae	IP	710	6.25	N	N	N	N	N	na
Plectodon regalis Marshall, 2002	Cuspidariidae	IP	805	6.1	Y	N	N	N	Y	na

Appendix. (Continued)

Species	Family	Zone[1]	Dep[2]	Size[3]	Live[4]	Anat[5]	Mol[6]	Anl[7]	Res[8]	Source[9]
Pseudogrippina wangellanica Marshall, 2002	Cuspidariidae	IP	437	2.8	Y	N	N	N	Y	na
Rhinoclama brooki Marshall, 2002	Cuspidariidae	IP	274	6.6	N	N	N	N	Y	na
Rhinoclama tangaroa Marshall, 2002	Cuspidariidae	IP	437	2.52	Y	N	N	N	N	na
Centrocardita pileolata Oliver and Holmes, 2004	Cyamiidae	IO	18	4	Y	N	N	N	Y	na
"Lutetina" capricornica Oliver and Holmes, 2004	Cyamiidae	IO	17	2	N	N	N	N	Y	na
Pseudokellia franki Zelaya and Ituarte, 2009	Cyamiidae	AN	100	4.2	Y	Yd	N	N	Y	NC
Peregrinamor gastrochaenans Kato and Itani, 2000	Gaimardiidae	NWP	int	6.4	Y	Yd	N	N	Y, H	na
Austrodevonia sharnae Middelfart and Craig, 2004	Galeommatidae	IP	int	4.4	Y	Y	N	N	Y, H	na
Duoconclavis piscator Middelfart, 2005	Galeommatidae	IP	int	5.2	Y	Yd	N	N	Y	R
Ephippodontomorpha hirsutus Middelfart, 2005	Galeommatidae	IP	na	9.9	Y	Yd	N	N	H	R
Galeomma phuketi Lützen and Nielsen, 2005	Galeommatidae	IP	int	6	Y	Y	N	N	Y	NC
Galeomma sagenata Oliver and Holmes, 2004	Galeommatidae	IO	18	4.81	Y	Y	N	N	Y	na
Nudiscintilla glabra Lützen and Nielsen, 2005	Galeommatidae	IP	int	6.8	Y	Yd	N	N	Y	NC
Parabornia palliopapillata Simone, 2001	Galeommatidae	WA	sh	10	Y	Yd	N	N	H	na
Scintilla macrodactylus Lützen and Nielsen, 2005	Galeommatidae	IP	sh	4.6	Y	Yd	N	N	Y	NC
Scintilla minor Lützen and Nielsen, 2005	Galeommatidae	IP	sh	4.3	Y	Y	N	N	Y	NC
Scintilla mortoni Lützen and Nielsen, 2005	Galeommatidae	IP	sh	5.3	Y	Yd	N	N	Y	NC
Scintilla ovalis Lützen and Nielsen, 2005	Galeommatidae	IP	sh	8.2	Y	Yd	N	N	Y	NC
Scintilla papillosa Lützen and Nielsen, 2005	Galeommatidae	IP	int	9.8	Y	Yd	N	N	Y	NC
Scintilla sannio Lützen and Nielsen, 2005	Galeommatidae	IP	sh	10.6	Y	Yd	N	N	Y	NC
Scintilla siamense Lützen and Nielsen, 2005	Galeommatidae	IP	na	11	Y	Yd	N	N	Y	NC
Scintilla unicornia Lützen and Nielsen, 2005	Galeommatidae	IP	sh	7.4	Y	Yd	N	N	Y	NC
Scintilla verrucosa Lützen and Nielsen, 2005	Galeommatidae	IP	int	6.8	Y	Yd	N	N	Y	NC
Troglodytoconcha carpentariensis Middelfart, 2005	Galeommatidae	IP	11	7.5	Y	Yd	N	N	Y, H	R
Aclistothyra orientalis Lützen and Nielsen, 2005	Galeommatidae	IP	na	10	Y	Yd	N	N	Y	NC
Scintilla agilis Lützen and Nielsen, 2005	Galeommatidae	IP	sh	6.1	Y	Yd	N	N	Y	NC
Scintilla larcombae Oliver and Holmes, 2004	Galeommatidae	IO	18	4	Y	Y	N	N	Y	na

Appendix. (Continued)

Species	Family	Zone[1]	Dep[2]	Size[3]	Live[4]	Anat[5]	Mol[6]	Anl[7]	Res[8]	Source[9]
Scintilla longitentaculata Lützen and Nielsen, 2005	Galeommatidae	IP	int	5.5	Y	Yd	N	N	Y	NC
Scintilla lynchae Oliver and Holmes, 2004	Galeommatidae	IO	1	10	Y	Y	N	N	Y	na
Glycymeris (Glycymeris) vanhensstumi Goud and Gulden, 2009	Glycymerididae	EA	110	50	Y	N	N	N	N	NC
Empressostrea kostini Huber and Lorenz, 2007	Gryphaeidae	IP	71	500	Y	Y	N	N	H	na
Neopycnodonte zibrowii Gofas, Salas, and Taviani in Wisshak *et al.*, 2009	Gryphaeidae	EA	500	300	Y	Y	N	N	Y	NC
Kelliella abyssicola Allen, 2001	Kelliellidae	EA,WA	4632	ca. 3	Y	Y	N	N	N	na
Kelliella biscayensis Allen, 2001	Kelliellidae	EA	1015	ca. 3	Y	Y	N	N	Y	na
Kelliella concentrica Allen, 2001	Kelliellidae	WA	811	ca. 3	Y	Yd	N	N	N	na
Kelliella elongata Allen, 2001	Kelliellidae	WA	5100	ca. 3	Y	Y	N	N	N	na
Kelliella tenina Allen, 2001	Kelliellidae	EA	1014	ca. 3	Y	Yd	N	N	Y	na
Kellia kussakini Kamenev, 2004b	Kelliidae	NWP	20	4.8	N	N	N	N	N	na
Scacchia rodguesensis Oliver and Holmes, 2004	Lasaeidae	IO	2	3	N	N	N	N	Y	na
Arthritica japonica Lützen and Takahashi, 2003	Leptonidae	NWP	int	2.05	Y	Yd	N	N	Y, H	na
Ctenoides miamiensis Mikkelsen and Bieler, 2003	Limidae	WA	501	13.6	Y	Y	N	N	N	R
Ctenoides obliquus Mikkelsen and Bieler, 2003	Limidae	WA	1335	40	Y	Yd	N	N	N	R
Ctenoides vokesi Mikkelsen and Bieler, 2003	Limidae	WA	732	60	N	N	N	N	N	R
Limatula bisecta Allen, 2004	Limidae	EA	479	2	Y	Y	N	N	Y	na
Limatula celtica Allen, 2004	Limidae	EA	4632	6	Y	Y	N	N	N	na
Limatula demiradiata Allen, 2004	Limidae	EA	330	3.6	Y	Y	N	N	Y	na
Limatula domaneschii de Castro Oliveira and Absalão, 2008	Limidae	WA	1044	1.2	N	N	N	N	Y	na
Limatula margaretae Allen, 2004	Limidae	EA,WA	4632	6	Y	Y	N	N	N	na
Limatula smithi Allen, 2004	Limidae	AN	3385	11.7	Y	Y	N	N	N	na
Limatula thalassae Allen, 2004	Limidae	EA	511	5.3	Y	Y	N	N	N	na
Limea argentineae Allen, 2004	Limidae	WA	993	6.5	Y	Y	N	N	Y	na
Limea lirata Allen, 2004	Limidae	WA	2095	2	Y	Y	N	N	Y	na
Limopsis oliveri Amano and Lutaenko, 2004	Limidae	NWP	218	11.1	N	N	N	N	E	na
Acesta maui Marshall, 2001	Limidae	IP	1172	185	Y	N	N	N	N	R
Acesta oophaga Järnegren, Schander, and Young, 2007	Limidae	WA	800	113	Y	Y	Y	P	Y, H	na
Acesta saginata Marshall, 2001	Limidae	IP	1650	116	Y	N	N	N	N	R
Limopsis marerubra Oliver and Zuschin, 2000	Limopsidae	IO	19	2.5	N	N	N	N	Y	NC
Nipponolimopsis littoralis Sasaki and Haga, 2007	Limopsidae	NWP	int	3	Y	Y	N	N	N	na
Aftolucina discontinua Cosel, 2006	Lucinidae	EA	230	18	Y	N	N	N	H	na
Anodontia aurora Taylor and Glover, 2005	Lucinidae	IP	90	12	N	N	N	N	Y	R
Anodontia blanquita Taylor and Glover, 2005	Lucinidae	EP	46	83	N	N	N	N	N	R

Appendix. (Continued)

Species	Family	Zone[1]	Dep[2]	Size[3]	Live[4]	Anat[5]	Mol[6]	Anl[7]	Res[8]	Source[9]
Anodontia chevalieri Cosel in Taylor and Glover, 2005[10]	Lucinidae	EA	3	42	N	N	N	N	N	R
Anodontia insulosa Taylor and Glover, 2005	Lucinidae	IP	47	30	N	N	N	N	N	R
Anodontia kora Taylor and Glover, 2005	Lucinidae	IO	sh	56	N	N	N	N	N	R
Anodontia senegalensis Cosel in Taylor and Glover, 2005[10]	Lucinidae	EA	230	37	N	N	N	N	N	R
Anodontia trulla Taylor and Glover, 2005	Lucinidae	IP	sh	52	N	N	N	N	Y	R
Anodontia tuticorina Taylor and Glover, 2005	Lucinidae	IO	46	24	N	N	N	N	Y	R
Bathyaustriella thionipta Glover, Taylor, and Rowden, 2004	Lucinidae	IP	500	48.5	Y	Yd	Y	P	Y, H	na
Bretskya scapula Glover and Taylor, 2007	Lucinidae	IP	140	6.9	N	N	N	N	N	NC
Cardiolucina undula Glover and Taylor, 2007	Lucinidae	IP	200	5	N	N	N	N	Y	NC
Divaricella chavani Cosel, 2006	Lucinidae	EA	6	28	N	N	N	N	N	na
Epicodakia nodulosa Glover and Taylor, 2007	Lucinidae	IP	58	15.2	N	N	N	N	N	NC
Ferrocina multiradiata Glover and Taylor, 2007	Lucinidae	IP	417	16.6	N	N	N	N	N	NC
Goniomyrtea avia Glover and Taylor, 2007	Lucinidae	IP	200	10	N	N	N	N	N	NC
Goniomyrtea fidelis Glover and Taylor, 2007	Lucinidae	IP	120	10.4	N	N	N	N	N	NC
Graecina colombiensis Taylor and Glover, 2009	Lucinidae	WA	366	51.6	N	N	N	N	Y	na
Graecina karinae Cosel, 2006	Lucinidae	EA	425	40	N	N	N	N	Y	na
Joellina dosiniformis Cosel, 2006	Lucinidae	EA	425	32	N	N	N	N	Y, H	na
Jorgenia gracile Taylor and Glover, 2009	Lucinidae	WA	600	43.7	N	N	N	N	Y	na
Jorgenia louisiana Taylor and Glover, 2009	Lucinidae	WA	555	60.7	N	N	N	N	H	na
Jorgenia luteophila Taylor and Glover, 2009	Lucinidae	WA	850	27.1	N	N	N	N	Y	na
Lamellolucina jawa Taylor and Glover, 2002	Lucinidae	IP	50	22	N	N	N	N	Y	R
Lamellolucina oliveri Taylor and Glover, 2002	Lucinidae	IO	285	21	N	N	N	N	N	R
Lamellolucina pilbara Taylor and Glover, 2002	Lucinidae	IO	30	22.8	Y	Y	N	N	Y	R
Lamellolucina trisulcata Taylor and Glover, 2002	Lucinidae	IP,IO	20	13.5	N	N	N	N	N	R
Lamylucina exgaini Cosel, 2006	Lucinidae	EA	sh	20	N	N	N	N	N	na
Lepidolucina belepia Glover and Taylor, 2007	Lucinidae	IP	42	12.5	N	N	N	N	Y	NC
Leucospiaera diapiana Glover and Taylor, 2007	Lucinidae	IP	250	5.3	N	N	N	N	N	NC
Liralucina craticula Glover and Taylor, 2007	Lucinidae	IP	8	3.8	N	N	N	N	Y	NC

Appendix. (Continued)

Species	Family	Zone[1]	Dep[2]	Size[3]	Live[4]	Anat[5]	Mol[6]	Anl[7]	Res[8]	Source[9]
Liralucina lifouina Glover and Taylor, 2007	Lucinidae	IP	30	6.9	Y	N	N	N	Y	NC
Liralucina vaubani Glover and Taylor, 2007	Lucinidae	IP	155	3.1	N	N	N	N	Y	NC
Lucinoma anemiophila Holmes, Oliver, and Sellanes, 2005	Lucinidae	EP	780	61	N	N	N	N	Y, H	NC
Lucinoma atalantae Cosel, 2006	Lucinidae	EA	2160	29	Y	N	N	N	Y, H	na
Lucinoma gagei Oliver and Holmes, 2006a	Lucinidae	IO	967	62	Y	Y	N	N	Y	na
Lucinoma kazani Salas and Woodside, 2002	Lucinidae	EA	1709	38.4	Y	Yd	N	N	Y	NC
Lucinoma myriamae Cosel, 2006	Lucinidae	EA	425	53	N	N	N	N	Y, H	na
Meganodontia acetabulum Bouchet and Cosel, 2004	Lucinidae	NWP	256	150	N	N	N	N	Y	na
Myrtina leptolira Glover and Taylor, 2007	Lucinidae	IP	200	14.9	N	N	N	N	N	NC
Myrtina porcata Glover and Taylor, 2007	Lucinidae	IP	174	10.3	Y	N	N	N	Y	NC
Neophysema aphanes Taylor and Glover, 2005	Lucinidae	EP	120	16.6	N	N	N	N	Y	na
Notomyrtea vincentia Glover and Taylor, 2007	Lucinidae	IP	200	7.7	N	N	N	N	Y	NC
Parvidontia laevis Glover and Taylor, 2007	Lucinidae	IP	59	10.9	N	N	N	N	Y	NC
Pilucina australis Glover and Taylor, 2001	Lucinidae	IO,IP	int	4.8	N	N	N	N	N	R
Pillucina copiosa Glover and Taylor, 2007	Lucinidae	IP	120	4.2	Y	N	N	N	Y	NC
Pillucina denticula Glover and Taylor, 2001	Lucinidae	IO	50	3.7	N	N	N	N	Y	R
Pillucina mauritiana Glover and Taylor, 2001	Lucinidae	IO	na	11.6	N	N	N	N	Y	R
Pillucina pacifica Glover and Taylor, 2001	Lucinidae	IP	30	8	N	N	N	N	N	R
Poumea coselia Glover and Taylor, 2007	Lucinidae	IP	70	8.5	N	N	N	N	Y	NC
Solelucina kanmacia Glover and Taylor, 2007	Lucinidae	IP	120	1.8	Y	Y	N	N	Y	NC
Tinalucina aequatorialis Cosel, 2006	Lucinidae	EA	98	6.8	N	N	N	N	Y	na
Nucinella boucheti La Perna, 2005	Manzanellidae	IP	1610	25	Y	N	N	N	Y	NC
Mysella gregaria Rotvit, Lützen, Jespersen, and Fox, 2007	Montacutidae	WA	int	6	Y	Yd	N	N	H	na
Mysella narchii Passos and Domaneschi, 2006	Montacutidae	AN	25	3.1	Y	Yd	N	N	Y	NC
Hunkydora rakiura Marshall, 2002	Myochamidae	IP	360	5.2	Y	N	N	N	N	na
Myadoropsis wairua Marshall, 2002	Myochamidae	IP	550	5.1	N	N	N	N	N	na
Bathymodiolus anteumbonatus Cosel, 2008a	Mytilidae	IP	1629	60	Y	Yd	Y	N	Y, H	NC
Bathymodiolus edisonensis Cosel, 2008a	Mytilidae	IP	1629	163	Y	Yd	N	N	Y, H	NC
Bathymodiolus hirtus T. Okutani, Fujikura, and Sasaki, 2004	Mytilidae	NWP	644	81.2	Y	Yd	N	N	Y, H	NC

Appendix. (Continued)

Species	Family	Zone[1]	Dep[2]	Size[3]	Live[4]	Anat[5]	Mol[6]	Anl[7]	Res[8]	Source[9]
Bathymodiolus manusensis Hashimoto and Furuta, 2007	Mytilidae	IP	1900	100.8	Y	Yd	Y	N	Y, H	NC
Bathymodiolus marisindicus Hashimoto, 2001	Mytilidae	IO	2450	86	Y	Yd	N	N	Y, H	NC
Bathymodiolus mauritanicus Cosel, 2002	Mytilidae	EA	1200	110	Y	N	N	N	Y	R
Bathymodiolus securiformis T. Okutani, Fujikura, and Sasaki, 2004	Mytilidae	NWP	642	135.1	Y	Yd	N	N	Y, H	NC
Bathymodiolus taiwanensis Cosel, 2008b	Mytilidae	NWP	355	56	Y	Yd	N	(P)	Y, H	NC
Bathymodiolus tangaroa Cosel and Marshall, 2003	Mytilidae	IP	1205	199.6	Y	Yd	N	N	N	na
Bathymodiolus tangaroa turkayi Cosel, 2008a	Mytilidae	IP	1629	120	Y	Yd	Y	N	Y, H	NC
Benthomodiolus geikotsucola T. Okutani and Miyazaki, 2007	Mytilidae	NWP	4037	43.5	Y	Yd	N	N	Y, H	na
Dacrydium leucoguttatum van der Linden and Moolenbeek, 2004	Mytilidae	WA	25	3	N	N	N	N	N	CK
Gigantidas gladius Cosel and Marshall, 2003	Mytilidae	IP	755	316	Y	Y	N	N	H	na
Gigantidas horikoshii Hashimoto and Yamane, 2005	Mytilidae	NWP	762	195.6	Y	Yd	N	N	Y, H	NC
Lithophaga punctata Kleemann and Hoeksema, 2002	Mytilidae	IP	sh	13.5	Y	N	N	N	N	NC
Musculus nipponicus Kuroda in T. Okutani, 2005	Mytilidae	NWP	53	8.1	N	N	N	N	N	na
Musculus panhai Moolenbeek, 2009	Mytilidae	IP	6	13.4	Y	N	N	N	N	NC
Rhomboidiella rodriguesensis Oliver and Holmes, 2004	Mytilidae	IO	int	3	Y	N	N	N	Y	na
Neilonella profunda T. Okutani and Fujiwara, 2005	Neilonellidae	NWP	7320	6.7	Y	N	N	N	Y	na
Epilepton elpis Allen, 2007	Neoleptonidae	WA	4833	1.04	Y	Y	N	N	N	na
Neolepton amatoi Zelaya and Ituarte, 2004	Neoleptonidae	EP	27	2.4	N	N	N	N	Y	R
Neolepton arjanbosi van der Linden, 2003	Neoleptonidae	EA	int	1.3	N	N	N	N	Y	CK
Neolepton bonaerense Zelaya and Ituarte, 2004	Neoleptonidae	WA	77	2.3	N	N	N	N	Y	R
Neolepton faberi van der Linden, 2003	Neoleptonidae	WA	45	1.9	N	N	N	N	N	CK
Neolepton georgianum Zelaya and Ituarte, 2003	Neoleptonidae	AN	94	3.4	Y	Y	N	N	Y	NC
Neolepton holmergi Zelaya and Ituarte, 2003	Neoleptonidae	AN	94	2.8	Y	Y	N	N	Y	NC
Neolepton moolenbeeki van der Linden, 2003	Neoleptonidae	EA,WA	125	1.8	N	N	N	N	N	CK
Neolepton peetersae van der Linden, 2003	Neoleptonidae	WA	25	2	N	N	N	N	N	CK
Neolepton profundorum Allen, 2000	Neoleptonidae	WA	2323	2.5	Y	Y	N	N	Y	na
Neolepton victor van der Linden, 2003	Neoleptonidae	EA	int	2.7	N	N	N	N	E	CK

Appendix. (Continued)

Species	Family	Zone[1]	Dep[2]	Size[3]	Live[4]	Anat[5]	Mol[6]	Anl[7]	Res[8]	Source[9]
Neolepton yangan Zelaya and Ituarte, 2004	Neoleptonidae	EP	27	2.6	N	N	N	N	Y	R
Crassostrea hongkongensis Lam and Morton, 2003	Ostreidae	NWP	sh	160	Y	N	Y	P	N	C
Pandora gorii Rolán and Hernandez, 2007	Pandoridae	EP	30	5.1	N	N	N	N	Y	na
Panacca chilensis Coan, 2000	Paralimyidae	EP	180	21	N	N	N	N	Y	na
Aequipecten comutatus peripheralis Dijkstra and Kilburn, 2001	Pectinidae	IO	500	20	N	N	N	N	N	NC
Anguipecten pacificus Dijkstra, 2002a	Pectinidae	IP	455	60	N	N	N	N	N	NC
Anguipecten simoneae Morrison and Whisson, 2009	Pectinidae	IO	440	3	Y	N	N	N	Y	C
Cyclochlamys austrina Dijkstra and Marshall, 2008	Pectinidae	IP	415	2.45	N	N	N	N	Y	R
Cyclochlamys bacata Dijkstra and Marshall, 2008	Pectinidae	IP	437	1.9	N	N	N	N	Y	R
Cyclochlamys delli Dijkstra and Marshall, 2008	Pectinidae	IP	1006	5	Y	N	N	N	Y	R
Cyclochlamys irregularis Dijkstra and Marshall, 2008	Pectinidae	IP	622	3	N	N	N	N	Y	R
Cyclochlamys munida Dijkstra and Marshall, 2008	Pectinidae	IP	415	2.15	N	N	N	N	Y	R
Cyclochlamys pileolus Dijkstra and Marshall, 2008	Pectinidae	IP	538	1.5	Y	N	N	N	Y	R
Cyclochlamys plectofilum Oliver and Holmes, 2004	Pectinidae	IO	17	2	N	N	N	N	Y	na
Cyclochlamys wanganellica Dijkstra and Marshall, 2008	Pectinidae	IP	133	2.55	Y	N	N	N	Y	R
Mirapecten tuberosus Dijkstra and Kilburn, 2001	Pectinidae	IO	70	41.6	Y	N	N	N	N	NC
Palliolum minutulum Dijkstra and Southgate, 2000	Pectinidae	IP	14	9.2	Y	N	N	N	N	NC
Veprichlamys africana Dijkstra and Kilburn, 2001	Pectinidae	IO	500	36	N	N	N	N	N	NC
Veprichlamys deynzerorum Dijkstra, 2004	Pectinidae	IP	40	43	Y	N	N	N	Y	na
Adacnarca polarsterni Egorova, 2003	Philobryidae	AC	405	7.7	Y	Yd	N	N	N	na
Cosa tholiatus Oliver and Holmes, 2004	Philobryidae	IO	18	1.60	N	N	N	N	Y	na
Cratis thylicus Oliver and Holmes, 2004	Philobryidae	IO	17	1.6	N	N	N	N	Y	na
Xylophaga bayeri R. Turner, 2002	Pholadidae	WA	365	8	Y	Yd	N	N	N	R
Xylophaga corona Voight, 2007	Pholadidae	EP	2701	8.5	Y	Yd	N	N	Y, H	NC
Xylophaga depalmai R. Turner, 2002	Pholadidae	WA	152	9.8	Y	Y	N	N	N	R
Xylophaga gerda R. Turner, 2002	Pholadidae	WA	2072	3	Y	Yd	N	N	N	R
Xylophaga heterosiphon Voight, 2007[11]	Pholadidae	EP	2750	1.3	Y	Yd	N	N	N	na
Xylophaga microchira Voight, 2007	Pholadidae	EP	2658	3.2	Y	Yd	N	N	N	na
Xylophaga muraokai R. Turner, 2002[11]	Pholadidae	EP	1615	14	Y	Yd	N	N	Y	R
Xylophaga oregona Voight, 2007	Pholadidae	EP	2211	8.2	Y	Yd	N	N	N	na
Xylophaga pacifica Voight, 2007	Pholadidae	EP	2700	6.3	Y	Yd	N	N	N	na

Appendix. (Continued)

Species	Family	Zone[1]	Dep[2]	Size[3]	Live[4]	Anat[5]	Mol[6]	Anl[7]	Res[8]	Source[9]
Xylophaga profunda R. Turner, 2002	Pholadidae	WA	1722	10.9	Y	N	N	N	Y	R
Xylophaga siebenalleri Voight, 2007	Pholadidae	EP	2750	6	Y	Yd	N	N	N	na
Xylophaga tipperi R. Turner, 2002	Pholadidae	WA	152	9	Y	Yd	N	N	Y	R
Xylophaga whoi R. Turner, 2002	Pholadidae	WA	914	14.9	Y	Y	N	N	N	R
Xylophaga zierenbergi Voight, 2007	Pholadidae	EP	3232	15.7	Y	Yd	N	N	Y	na
Xylopholas crooki Voight, 2007	Pholadidae	EP	2656	1.5	Y	Yd	N	N	Y	na
Xylopholas scrippsorum Voight, 2007	Pholadidae	EP	2400	4.4	Y	Yd	N	N	N	na
Cetomya bacata Krylova, 2001	Poromyidae	IP	694	12.8	Y	Y	N	N	N	NC
Cetomya celsa Krylova, 2001	Poromyidae	IP	1980	10.3	Y	Yd	N	N	N	NC
Cetomya nataliae Krylova, 2001	Poromyidae	IP	800	9.4	Y	Y	N	N	N	NC
Cetomya poutiersi Krylova, 2001	Poromyidae	IP	490	97	Y	Yd	N	N	N	NC
Cetomya voskresenskii Krylova, 2001	Poromyidae	IP	980	13.2	Y	Yd	N	N	N	NC
Dilemma japonicum Sasaki and Leal, 2008	Poromyidae	NWP	273	9.3	N	N	N	N	Y	na
Ledella marisnostri La Perna, 2004	Pristiglomidae	EA	976	2.27	N	N	N	N	E	CK
Catillopecten tasmani Dijkstra and Marshall, 2008	Propeamussiidae	IP	1373	10	Y	N	N	N	Y	R
Cyclopecten capverdensis Dijkstra and Goud, 2002	Propeamussiidae	EA	610	7	N	N	N	N	Y	NC
Cyclopecten cincinnatus Dijkstra and Gofas, 2004	Propeamussiidae	EA	845	5	Y	N	N	N	H	NC
Cyclopecten fluctuosus Dijkstra and Marshall, 2008	Propeamussiidae	IP	1799	6.55	Y	N	N	N	Y	R
Cyclopecten textus Dijkstra and Marshall, 2008	Propeamussiidae	IP	2830	12.5	N	N	N	N	Y	R
Cyclopecten vimineus Dijkstra and Gofas, 2004	Propeamussiidae	EA	1500	15	N	N	N	N	H	NC
Parvamussium aldeynzeri Dijkstra, 2004	Propeamussiidae	IP	bat	10	N	N	N	N	Y	na
Parvimussium cancellorum Dijkstra and Marshall, 2008	Propeamussiidae	IP	774	7	N	N	N	N	Y	R
Parvamussium intuslaevis Dijkstra and Gofas, 2004	Propeamussiidae	EA	325	5	N	N	N	N	H	NC
Parvamussium musorstomi Dijkstra, 2001	Propeamussiidae	IP	500	8	N	N	N	N	Y	NC
Parvamussium richer Dijkstra, 2001	Propeamussiidae	IP	591	13	Y	N	N	N	E	NC
Parvamussium toyoshiomarnae T. Okutani, 2005	Propeamussiidae	NWP	311	10.5	N	N	N	N	N	na
Similipecten redferni Dijkstra, 2002b	Propeamussiidae	WA	60	4.5	N	N	N	N	Y	NC
Sinepecten segonzaci Schein, 2006[12]	Propeamussiidae	IP	1674	28	Y	N	N	N	Y, H	na
Gari juliae Willan and Huber, 2007	Psammobiidae	IP	60	36	N	N	N	N	N	na
Gari sharabatiae Rusmore-Villaume, 2005	Psammobiidae	IO	na	25.5	N	N	N	N	E	CK
Abra aegyptiaca Oliver and Zuschin, 2000	Semelidae	IO	40	4	N	N	N	N	N	na
Abrina scarlatoi Kamenev, 2004a	Semelidae	NWP	120	11.2	N	N	N	N	N	na
Solemya (Petrasma) miuraensis Kanie and Kuramochi, 2002	Solemyidae	NWP	20	53.3	N	N	N	N	Y	na
Solemya notialis Simone, 2009a	Solemyidae	WA	33.5	12.9	Y	Yd	N	N	Y	na
Solemya tagiri T. Okutani, Hashimoto, and Miura, 2004	Solemyidae	NWP	116	23.8	Y	Y	N	N	Y, H	NC
Solen darwinensis Cosel, 2002b	Solenidae	IP	sh	83.6	N	N	N	N	E	R

Appendix. (Continued)

Species	Family	Zone[1]	Dep[2]	Size[3]	Live[4]	Anat[5]	Mol[6]	Anl[7]	Res[8]	Source[9]
Solen kikuchii Cosel, 2002b	Solenidae	NWP	49	25.9	Y	Y	N	N	N	R
Solen pseudolinearis Cosel, 2002b	Solenidae	NWP	sh	64.1	N	N	N	N	Y	R
Solen sarawakensis Cosel, 2002b	Solenidae	IP	sh	134	Y	Y	N	N	N	R
Solen soleneae Cosel, 2002b	Solenidae	NWP,IO	sh	39.5	N	N	N	N	N	R
Solen thachi Cosel, 2002b	Solenidae	IP	sh	75.7	N	N	N	N	N	R
Solen thailandicus Cosel, 2002b	Solenidae	IP	sh	48.9	Y	Y	N	N	Y	R
Grippina acherontis Marshall, 2002	Spheniopsidae	IP	40	2.45	Y	N	N	N	Y	na
Grippina globosa Marshall, 2002	Spheniopsidae	IP	550	1.43	Y	N	N	N	Y	na
Grippina pumila Marshall, 2002	Spheniopsidae	IP	183	2.8	Y	N	N	N	N	na
Grippina punctata Marshall, 2002	Spheniopsidae	IP	805	2.15	Y	N	N	N	N	na
Grippina rex Marshall, 2002	Spheniopsidae	IP	805	5.1	Y	N	N	N	E	na
Grippina spirata Marshall, 2002	Spheniopsidae	IP	200	2.05	Y	N	N	N	N	na
Spondylus cevikeri Lamprell, Stanisic, and Clarkson, 2001b	Spondylidae	EA	10	80.7	N	N	N	N	N	R
Spondylus deforgesi Lamprell and Healy, 2001	Spondylidae	IP	100	34.8	N	N	N	N	Y	NC
Spondylus exiguus Lamprell and Healy, 2001	Spondylidae	IP	140	6.4	N	N	N	N	Y	NC
Spondylus heidkeae Lamprell and Healy, 2001	Spondylidae	IO,IP	110	45	N	N	N	N	N	NC
Spondylus maestratii Lamprell and Healy, 2001	Spondylidae	IP	60	45.5	N	N	N	N	N	NC
Spondylus mireilleae Lamprell and Healy, 2001	Spondylidae	IP	460	72.3	N	N	N	N	N	NC
Spondylus orstomi Lamprell and Healy, 2001	Spondylidae	IP	318	48.5	N	N	N	N	Y	NC
Spondylus proneri Lamprell and Healy, 2001[12]	Spondylidae	IP	900	30.9	Y	N	N	N	N	NC
Spondylus rippingalei Lamprell and Healy, 2001	Spondylidae	IO,IP	49	4	N	N	N	N	N	NC
Spondylus swinneni Lamprell, Stanisic, and Clarkson, 2001a	Spondylidae	IP	50	125	N	N	N	N	N	na
Macoma biota Arrua and Domaneschi, 2005	Tellinidae	WA	int	53.4	Y	Yd	N	N	Y	NC
Semelangulus mesodesmoides Oliver and Zuschin, 2000	Tellinidae	IO,IP	10	8	N	N	N	N	N	NC
Asthenothaerus maxwelli Marshall, 2002	Thraciidae	IP	293	46	N	N	N	N	N	na
Parvithracia ampla Marshall, 2002	Thraciidae	IP	1019	6.5	N	N	N	N	N	na
Parvithracia fragilissima Marshall, 2002	Thraciidae	IP	1386	7.9	Y	N	N	N	N	na
Parvithracia lukini Kamenev, 2002	Thraciidae	NWP	418	11	Y	Y	N	D	N	na
Parvithracia melchior Marshall, 2002	Thraciidae	IP	805	11.5	N	N	N	N	N	na
Parvithracia sirenkoi Kamenev, 2002	Thraciidae	NWP	920	8.9	Y	Y	N	D	N	na
Thracia arienatoma Oliver and Holmes, 2004	Thraciidae	IO	na	3	Y	N	N	N	Y	na
Trigonothracia mimica Marshall, 2002	Thraciidae	IP	415	3.95	Y	N	N	N	N	na
Adontorhina keegani Barry and McCormack, 2007	Thyasiridae	EA	789	0.98	Y	Yd	N	N	Y	NC
Adontorhina similis Barry and McCormack, 2007	Thyasiridae	EA	382	1.25	Y	Yd	N	N	N	NC

Appendix. (Continued)

Species	Family	Zone[1]	Dep[2]	Size[3]	Live[4]	Anat[5]	Mol[6]	Anl[7]	Res[8]	Source[9]
Axinus cascadiensis Oliver and Holmes, 2007	Thyasiridae	EP	2592	23.6	Y	Yd	N	N	Y, H	NC
Conchocele novaeguinensis K. Okutani, 2002	Thyasiridae	IP	470	73.9	N	N	N	N	Y	NC
"Leptaxinus" indusarium Oliver and Levin, 2006	Thyasiridae	IO	1000	5	Y	Y	N	N	Y	NC
Spinaxinus sentosus Oliver and Holmes, 2006b	Thyasiridae	EA	1160	16.5	Y	Y	N	N	Y	NC
Thyasira methanophila Oliver and Sellanes, 2005	Thyasiridae	EP	780	29.7	Y	Y	N	N	H	na
Thyasira scotiana Zelaya, 2009	Thyasiridae	AN	na	10	Y	Y	N	N	Y	na
Thyasira southwardae Oliver and Holmes, 2006b	Thyasiridae	AC	3040	16.7	Y	Y	N	N	Y, H	NC
Thyasira volcolutre Rodrigues and Oliver in Rodrigues, Oliver, and Cunha, 2008	Thyasiridae	EA	2200	17.2	Y	Yd	Y	P	H	NC
Diplodonta bogii Van Aartsen, 2004[13]	Ungulinidae	EA	na	10	N	N	N	N	N	na
Diplodonta moolenbeeki Van Aartsen and Goud, 2006	Ungulinidae	EA	na	25	N	N	N	N	N	R
Bonartemis amamiensis T. Okutani, 2005	Veneridae	NWP	126	20.5	N	N	N	N	Y	na
Lioconcha berthaulti Lamprell and Healy, 2002	Veneridae	IP	53	31.7	N	N	N	N	Y	NC, R
Lioconcha macaulayi Lamprell and Healy, 2002	Veneridae	IP	4	47.4	N	N	N	N	Y	NC, R
Lioconcha pseudofastigiata Lamprell and Healy, 2002	Veneridae	IP	sh	43.7	N	N	N	N	Y	NC, R
Lioconcha schioettei Lamprell and Healy, 2002	Veneridae	IP	52	42.1	N	N	N	N	N	NC, R
Microcirce consternana Oliver and Zuschin, 2001	Veneridae	IO	30.5	3.3	Y	Y	N	N	N	na
Spinosipella agnes Simone and Cunha, 2008	Verticordiidae	WA	900	22	N	N	N	N	N	R
Spinosipella tinga Simone and Cunha, 2008	Verticordiidae	WA	253	16.9	N	N	N	N	N	R
Verticordia ouricuri de Castro Oliveira and Absalão, 2009	Verticordiidae	WA	1950	4.5	N	N	N	N	Y	R
Callogonia cyrili Cosel and Salas, 2001	Vesicomyidae	EA	1805	26	N	N	N	P	Y	NC
Callogonia mauritanica Cosel and Salas, 2001	Vesicomyidae	EA	1200	7.6	N	N	N	P	Y	NC
Calyptogena (Archivesica) edisonensis T. Okutani, Kojima, and Kim, 2004	Vesicomyidae	IP	1483	99.8	Y	N	N	N	Y, H	NC
Calyptogena (Archivesica) magnocultellus K. Okutani, Kojima, and Iwasaki, 2002	Vesicomyidae	NWP	2535	198	N	N	N	N	Y	NC
Calyptogena (Archivesica) tsubasa T. Okutani, Fujikura, and Kojima, 2000	Vesicomyidae	NWP	3800	212.1	N	N	Y	N	Y	NC

Appendix. (Continued)

Species	Family	Zone[1]	Dep[2]	Size[3]	Live[4]	Anat[5]	Mol[6]	Anl[7]	Res[8]	Source[9]
Calyptogena (Ectenagena) fossajaponica T. Okutani, Fujikura, and Kojima, 2000	Vesicomyidae	NWP	6809	31.9	N	N	N	N	Y	NC
Calyptogena gallardoi Sellanes and Krylova, 2005	Vesicomyidae	EP	760	45	N	N	N	N	Y, H	NC
Calyptogena garuda T. Okutani and Soh, 2005	Vesicomyidae	IP	2064	237	N	N	N	N	Y	na
Isorropodon bigoti Cosel and Salas, 2001	Vesicomyidae	EA	1200	21	Y	Y	N	P	N	NC
Isorropodon curtum Cosel and Salas, 2001	Vesicomyidae	EA	1200	11.3	N	N	N	P	Y	NC
Vesicomya crenulomarginata Okutani, Kojima, and Iwasaki, 2002	Vesicomyidae	NWP	2517	47	N	N	N	N	Y	NC
Vesicomya kaikoae K. Okutani, Fujikura, and Kojima, 2000	Vesicomyidae	NWP	3760	42.3	N	N	N	N	Y	NC
Vesicomya kuroshimana K. Okutani, Fujikura, and Kojima, 2000	Vesicomyidae	NWP	812	58.9	N	N	N	N	Y	NC
Waisiuconcha haeckeli Cosel and Salas, 2001	Vesicomyidae	EA	1200	4	Y	N	N	P	Y	NC
Yoldiella dautzenbergi La Perna, 2008	Yoldiidae	EA	1360	4.08	N	N	N	N	Y	na
Yoldiella kaikonis T. Okutani and Fujiwara, 2005	Yoldiidae	NWP	7333	6.6	Y	Yd	N	N	Y	na
Yoldiella ovulum La Perna, 2004	Yoldiidae	EA	1500	1.9	N	N	N	N	E	CK
Yoldiella thaerella Killeen and J. Turner, 2009	Yoldiidae	AC	2900	3.6	Y	Y	N	N	N	NC
Yoldiella wareni La Perna, 2004	Yoldiidae	EA	2000	1.51	N	N	N	N	E	CK

[1] Zones: AC, Arctic; AN, Antarctic; EA, eastern Atlantic; EP, eastern Pacific; IO, Indian Ocean; IP, Indo-West Pacific; NWP, northwestern Pacific; WA, western Atlantic.

[2] Dep: maximum recorded depth (m) for live- and dead-collected specimens; bat, bathyal; int, intertidal; sh, shallow.

[3] Size: maximum recorded dimension.

[4] Live: original material includes live-collected specimens.

[5] Anat: original description includes anatomical characters; Yd, anatomical characters are diagnostic for the new species.

[6] Mol: original description includes molecular characters.

[7] Anl: original description publication includes an analysis; D, discriminant; P, phylogenetic; (P), new species related to a previous phylogenetic analysis.

[8] Res: species is restricted to a particular geographical distribution (Y) or habitat (H); E, stated as "endemic" in the original description.

[9] Source: source of the new material; C, commercial harvesting or aquaculture; CK, in context of revision of a regional checklist; NC, new collections; R, in context of a taxonomic revision (in some cases regional).

[10] Redescribed by Cosel (2006).

[11] Additional data from Voight (2009).

[12] Additional data from Dijkstra and Marshall (2008).

[13] Additional data from van Aartsen and Goud (2006).